

The Claustrum, the External Capsule and the Extreme Capsule of *Macaca mulatta*¹

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The claustrum is a sheet of gray matter situated between the putamen and the insular cortex. The external capsule borders the claustrum medially and separates it from the putamen. Interposed between the claustrum and the island is the extreme capsule. Most of the interest in the claustrum in past years has centered in ontogenetic and phylogenetic studies. No agreement has been reached amongst the various investigators as to its significance and much controversy still exists.

At present, the knowledge of the fiber connections of the claustrum is incomplete. The ways in which the basal ganglia and the insular cortex are related to the claustrum and its surrounding capsules present interesting problems. One might speculate that the claustrum serves as a relay in the discharge, directly or by way of the basal ganglia, from the supplementary motor areas of the cortex to the tegmentum of the midbrain.

The two capsules that bound the claustrum have also not been completely evaluated. There is no consensus regarding the functional significance or the fiber components of the external and the extreme capsules and the claustrum.

REVIEW OF PERTINENT LITERATURE

Various earlier controversial theories regarding the development of the claustrum have been reviewed by Ariëns Kappers, Huber, and Crosby ('36). Meynert (1884), Brodmann, ('09), Sterzi ('15), and Rose ('28) considered the claustrum a derivation of the insular cortex. Brodmann ('09) regarded it as a duplication of the deepest layer of this cortex. Ernst de Vries ('10) felt that the claustrum was a part of the neopallium, drawn out subcortically to ex-

tend beneath the rhinencephalic sulcus (Ariëns Kappers, '08; de Vries, '10).

According to Landau ('19) and Faul ('26), the claustrum arises from a ventricular matrix, located at the palliostriatal angle. This gray mass migrates ventrolateralward to lie behind the lower margin of the neocortex and underneath the rhinencephalic cortex. Due to the neurobiotaxic influence of the ascending fibers of the lateral forebrain bundle, the anlage of the claustrum becomes plate-like in configuration. These last authors regarded the claustrum as independent of both the striatum and the cortex, since their embryological studies showed no connection of the island with the claustrum during ontogenesis. This fact would not favor the theory advocated by Meynert (1884), Brodmann ('09) and Rose ('28) that the claustrum is a derivative of the insula. Moreover, Landau ('23) reported a human case in which the insula was absent in the presence of an ipsilateral claustrum and Dodgson ('55) described a congenitally malformed human brain in which the insula was present in the absence of the ipsilateral dorsal claustrum. Furthermore, Macchi ('51) showed that the claustrum is developed before the island becomes differentiated.

The topographical anatomy of the claustrum has been described by Rose ('28), Klingler ('41), Macchi ('41, '47), and Källén ('51), and was reviewed by Rae ('54a). The claustrum has been divided into a compact dorsal part, situated between the putamen and the insular cortex, and a ventral portion, which projects forward into the white matter of the superior

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temporal lobe (Macchi, '51; Rae, '54b). The ventral claustrum is broken up into scattered masses of gray by the fibers of the anterior commissure and by the unciniate fasciculus (Papez, '45). Landau ('36, '37, '38) described a claustral extension beyond the island which he termed the claustrum parvum. Kuhlénbeck ('24) stated that the claustrum was fused with the anterior perforated substance. Whitaker ('21) found macroscopic continuity between the claustrum and the amygdaloid nucleus. However, the claustral-amygdaloid connections have been denied by Völsch ('06), Hilpert ('28), and Brockhaus ('38). Nevertheless it is generally considered that portions of the ventral claustrum lie adjacent to the amygdala, the superior temporal gyrus, and the ventral part of the frontal lobe (Rae, '54a).

A detailed study of the microscopic structure of the human claustrum was made by Rae ('54a). Other descriptions of the microscopic anatomy of this region have been reported by Pintus ('30, '31), Brockhaus ('38, '40), and Macchi ('48). The dorsal and the ventral claustrum are histologically similar. Silver preparations show a network of fine and medium-sized fiber fascicles extending in various planes, with the bodies of the claustral cells in the interstices. The cell bodies are triangular, ovoid, fusiform or pyramidal in shape, with the fusiform cells most numerous near the external and extreme capsules, and the other types distributed at random (Rae, '54a). The fusiform cells, which are typically oriented with their greatest diameters in the vertical plane, have been studied by several observers (V. Bechterew, 1899; Spiegel, '19; Kuhlénbeck, '24). The large number of this type of cell is regarded as characteristic of the claustrum.

In the literature to date, scanty information has accumulated concerning the fiber connections of the claustrum and much controversy still exists concerning those connections which have been reported. An exchange of fibers between the external capsule and the lateral border of the putamen has been described by Wilson ('14), Kodama ('27), Pintus ('32), Macchi ('48), and Rae ('54a). These fibers are not numerous in any one field, however, and it is uncertain whether any of them arise in

the claustrum. Fibers from the insular cortex enter the extreme capsule and some of them continue medially to become intermingled with the claustral network (Rae, '54a). Interconnections between the claustrum and the insular cortex have been described by Berlucchi ('27) and by Kató ('38) in the cat, by Mettler ('45) in the mangabey, and by Rae ('54a) in human material. However, similar studies on the human brain by Cajal ('02), Pintus ('32), and Macchi ('48) failed to reveal these fascicles.

Destruction of the frontal cortex anterior to the motor area in monkeys produced degeneration in the claustrum according to Bianchi ('22) and lesions in areas 9 and 11 of the macaques permitted demonstration of fiber connections to the claustrum, according to Mettler ('35a, '47). Continuity between the ventral claustrum and the gyrus olfactorius lateralis was noted by von Economo in 1929. Macchi ('48, '51), Landau ('19), and Rose ('28) described connections of the claustrum with the olfactory area. These were disputed by Spiegel ('19) and by Brockhaus ('40). Berlucchi (cat, '27) and Papez (man, '45) demonstrated fibers originating from the piriform cortex and passing around the frontal surface of the amygdala to reach the claustrum.

Hirasawa and coworkers ('38) described fibers from area 22 of the temporal cortex to the claustrum, in support of Völsch's ('10) contention that the claustrum of apes had fiber connections with the temporal lobe. Macroscopic continuity between the ventral claustrum and the amygdaloid nucleus has been reported (Pintus, '31; Macchi, '48), although no fiber connections have been found. However, in *Didelphis*, van der Sprengel ('26) reported fibers in the lateral olfactory nucleus, which reached the contralateral external capsule and the claustrum by way of the anterior commissure. This statement was supported by Fox, McKinley and Magoun ('44), who stimulated the lateral part of the olfactory bulb in the cat and recorded positive potentials in the claustrum. Le Gros Clark and Meyer ('47) removed the olfactory bulb but were unable to find degeneration in the claustrum of the rabbit.

Claustronigral or claustrategmental connections were suggested by the experimental lesions of Rosegay ('44) in the cat. Recruiting waves have been displayed in the claustrum from stimulation of the centromedian and the interlaminar nuclei of the dorsal thalamus (Starzl and Magoun, '51).

Many theories have been presented regarding the functions of the claustrum and these have been well summarized by Rae ('54b). Certain observers (Randacio, 1882; Kuhlenbeck, '24; Macchi, '48, '51) have considered the claustrum as part of the olfactory complex. Physiological evidence (Fox et al., '44; Rae, '54b; Segundo and Machne, '56) suggests that this area is a correlation center for olfacto-visceral-somatic impulses. Pintus ('32) and Landau ('36) believed that the claustrum is related to the production of speech. Ariëns Kappers ('08) felt that the claustrum exerts some effect upon motor responses, a conclusion which has been supported by the results of Mettler et al. ('39) and Kaada ('51), who found that movements evoked from cortical excitation were inhibited when the claustrum was stimulated.

Enclosing the claustrum are the extreme capsule, laterally, and the external capsule, medially. These capsules consist of dense, medium-sized and fine fibers, coursing in many planes. These fibers form a plexus in which are found a few fusiform and ovoid cells. The capsules contain association fibers from the superior and the inferior longitudinal fasciculi, the uncinata fasciculus, and the pyriform cortex (Papez, '29; Mettler, '35b; Ariëns Kappers, Huber, and Crosby, '36; Lockard, '48; Bucy and Klüver, '55).

Commissural fibers to the claustrum from the corpus callosum and the anterior commissure have been reported in many animals by Papez ('29), in rodents by Young ('36), in the bat by Humphrey ('35, '36), and in the macaque by Lauer ('45). Marchi degeneration granules have been traced from the anterior commissure to the external capsule by Fox and Schmitz ('43) and from the temporal lobe to the anterior commissure by Garol ('42a). The anterior limb of the anterior commissure enters the external capsule and is dispersed within it, forming an important part of this cap-

sule (Dejerine, 1895; E. Smith, '31; Lauer, '45).

The geniculotemporal bundle and the ventral thalamic radiations contribute fibers to the capsules. Vestibular and olfactory fibers (Papez, '45) have also been described. Temporal projection fibers in the extreme capsule have been noted (Bucy and Klüver, '55). Fibers from the inferior thalamic peduncle turn into the basal claustral complex. Other projection fibers from the ipsilateral motor cortex (Hirasawa and Kariya, '36) are contained within the capsules. Whether any of these fibers terminate in the claustrum has not been determined. Fibers of the ansa lenticularis originating in the caudate nucleus have been regarded by Foix and Nicolesco ('25) as passing in the external capsule with some termination in the claustrum.

MATERIALS AND METHODS

In this investigation, the experimental subjects used were monkeys (*Macaca mulatta*). Nine animals, with weights ranging between 2 and 7.2 kilograms, were chosen without preference for sex. A physical examination and a neurological testing were performed prior to each experimental procedure in order to insure the selection of active, alert, and healthy animals.

The destruction of one or more portions of the brain of each animal was achieved by cortical ablation or by electrical coagulation. The anesthetic for these operative procedures was diethyl ether, administered either by open drop method or by placing cotton saturated with ether in close proximity to the nasal and the oral passages. No preoperative medication was employed. The experiments were performed using sterile technique.

The stimulation of the surface cortex was carried out through the use of a Grass Stimulator, Model 3C. Square wave impulses, of one millisecond duration, at the frequency of 40 cycles per second, and with an intensity varying from 3 to 7 volts, were employed for cortical excitations. Lesions deep within the brain were made according to selected coordinates (Atlas and Ingram, '37) using a Lab-Tronics Stereotaxic Instrument (Model 4) for delivering a direct current of 300 micro-

amperes for 60 seconds through a unipolar electrode. A rectal plug served as the ground.

Daily observations were made and testing performed postoperatively to determine the effects of the experimental procedures. Particular attention was given to differences in behavior, changes in extra-ocular movements, and impairment of motor function, if such occurred. Each monkey was examined for spasticity, rigidity, and inequality of tonus in the extremities. Responses to auditory and visual stimuli were assessed.

After a 10–17 day period of observation, the animal was sacrificed with an overdose of Evipal, given intraperitoneally, and perfused with 1000 to 1200 ml of 10% formalin after insertion of a canula through the left ventricle into the ascending aorta.

The brain was allowed to harden for three to 7 days in three changes of 10% formalin and then, in most cases, photographs of the gross brain showing the location of the lesions were taken. The material was then prepared by the Marchi method (Swank and Davenport modification, '34, '35; Davenport and Swank, '35; M. Smith, '56). Normal material of the macaque brain stained by the Weil or pyridine-silver methods or with cresyl violet was available for comparison from the Huber Neurological Collection. The Riley Atlas ('43) proved a very useful aid in identifying some of the tracts and nuclei.

EXPERIMENTAL OBSERVATIONS

Protocol for monkey 1

A right frontoparietal craniotomy was performed upon a 3.6-kg male macaque. The central fissure was visualized and cortical ablation of right area 6 was then carried out by means of a surgical aspirator.

The animal tolerated the procedure well. During the next two weeks, he was active and alert. No paralysis, paresis, or inequality of tonus of the extremities could be detected. No other neurological abnormality was found on testing.

Ablation of left area 6 was then carried out following a left frontoparietal craniotomy. Again the animal tolerated the second procedure well, but revealed, on

subsequent examination, an unwillingness to use his right upper extremity in running. He was able to grasp weakly with the affected limb when climbing. This extremity also showed a decrease in tonus, but was not flaccid. Periodic testing over the next two weeks showed constant improvement with a gradual return to normal tone and use of the affected extremity. However, the right wrist was carried in a slightly extended position.

Two weeks after the second procedure, the animal was sacrificed and the brain perfused and prepared for microscopic study by the Marchi technique. When the brain had been removed from the cranium, gross inspection showed a right frontal lesion involving area 6 and part of areas 8 and 9 (fig. 1). Destruction of left area 6 and part of area 4 were noted (fig. 1). These lesions involved the superficial cortex and extended into the underlying white matter.

Microscopic observation showed lesions in areas 8 and 9 on the dorsolateral and medial surfaces of the right superior frontal gyrus and in the rostral end of the cingulate gyrus. These injuries involved the superficial cortex and the underlying white matter. The destruction extended caudally to include a portion of the premotor cortex. A diffuse, fine degeneration spread throughout the frontal cortex at the rostral border of this lesion and extended, by way of the corpus callosum, into the corresponding regions of the opposite hemisphere. Coarse and fine granules could be traced from the corona radiata, the subcallosal bundle and cingulate gyrus into, and throughout, the head of the caudate nucleus. Fine granules in the dorsal tip of the cingulum spread backward and forward along short association bundles. Bundles of fibers were traced through the head of the caudate nucleus into the putamen by way of the gray bridges connecting the two areas (fig. 13).

Contributions from the anterior limb of the internal capsule to the putamen were also noted. In the putamen some fibers terminated; others gradually worked their way medialward, through the globus pallidus and throughout the zona incerta and nucleus of the field of Forel as components of the lenticular fasciculus to discharge

directly to the red nucleus and tegmental gray around it (fig. 14). Still other bundles coursed ventrally to enter the ansa lenticularis and distribute with it to the pars ventralis of the deep midbrain tegmental gray and into tegmental cell groups caudal to the red nucleus. To this system were added corticotegmental fibers from the area of the lesion which traversed the internal capsule to enter the globus pallidus directly where some fibers ended. Many of these were corticorubral and corticotegmental fibers, which continued to the red nucleus and the dorsolateral, lateral and ventrolateral tegmental areas around the red nucleus by way of the lenticular fasciculus (fig. 15) and the ansa lenticularis. Corticotegmental fibers carried in the internal capsule, also coursed through the lateral thalamic nuclei and nucleus ventralis posterior pars lateralis to reach the red nucleus and the ventrolateral, lateral and dorsolateral tegmentum near this nucleus (fig. 14).

Degenerated fascicles were also followed from the whole length of the lesion into the right corona radiata and then into the region where the external and the extreme capsules adjoin each other. Fibers in the extreme capsule coursed ventrally and caudoventrally over the uncinata fasciculus into the superior and the middle temporal gyri. Other degenerated cortical association fibers were traced to the inferior temporal and hippocampal gyri. These cortical association fibers were augmented by some fascicles passing, a few at a time, from the external capsule through the dorsal claustrum into the extreme capsule. Whether any of these fibers terminated within the claustrum could not be ascertained due to their paucity and extremely fine myelination. Several small bundles in the extreme capsule passed laterally into the insular cortex but could not be followed for any great distance.

In addition to the cortical association fibers, some Marchi granules were traced rostrocaudally in the extreme capsule to its confluence with the external capsule at the posterior part of the lenticular nucleus (fig. 16). Together with fibers in the external capsule, they were projected directly into the tegmentum of the midbrain. However, most of the fibers contained in

the extreme capsule were cortical association fibers.

All along the course of the lesion, fibers were distributed from areas 8 and 9 into the external capsule. Some granules could be seen ventrally within the capsular boundary. A few degenerated fibers turned medially into the putamen. However, the majority of the degenerated fascicles coursed caudally within the external capsule at the junction of the two capsular systems behind the putamen (fig. 16). Nevertheless, contributions from the extreme capsule were traced a few at a time, through the claustrum into the external capsule. At the posterior end of the putamen, fibers from the deep white matter at parietal levels swept obliquely into the external capsule and passed medially behind the lenticular nucleus into the combined external and extreme capsules. Other fibers continued ventrally, in an oblique sublenticular or postlenticular course. Then they turned above the capsule of the lateral geniculate nucleus (fig. 17) to join corticotegmental fibers passing through the internal capsule into the ansa lenticularis and discharged, as a common bundle, into the dorsolateral, the lateral, and the ventrolateral tegmental areas around the red nucleus. A few fibers were traced into the substantia nigra.

The lesion in the left hemisphere destroyed the dorsomedial and the dorsolateral surfaces of the superior frontal gyrus, involving superficial cortex and adjacent white matter of the premotor area. Posteriorly, it extended into the motor cortex. Some degenerated medium-sized and coarse fibers could be traced through the corona radiata into the anterior limb of the internal capsule; others spread throughout the white matter of the frontal lobe. Commissural fibers coursed by way of the corpus callosum into the contralateral hemisphere but could not be followed to their terminations due to the bilaterality of the lesions.

Fibers from the corona radiata entered the head of the caudate nucleus. These fibers were less numerous than those entering the caudate nucleus from the more rostral lesion of the opposite side. The granules were traced throughout the anterior limb of the internal capsule in the gray

bridges to the putamen where some fibers ended. Many fibers continued medially into the globus pallidus and, through it, into the ansa lenticularis and the lenticular fasciculus. Over these fasciculi they discharged into the red nucleus itself, and into the dorsolateral, lateral and ventrolateral tegmentum around this nucleus (fig. 14). To this system were added corticotegmental fibers which passed by way of the internal capsule directly into the tegmentum. Additional fibers from the corona radiata entered the dorsal thalamic peduncle and, intermingling with the fibers of this peduncle, coursed through the lateral edge of the lateral thalamic nuclei and across the nucleus ventralis posterior pars lateralis into the red nucleus and the tegmentum around it.

Degeneration granules were followed from the site of the lesion into the region of continuity of the external and the extreme capsules. Through the latter, cortical association fibers distributed to the superior, the middle, the inferior temporal, and the hippocampal gyri. From the external capsule, a few degenerated fibers, presumably association bundles, were added to the extreme capsule by passing through the dorsal claustrum and appeared to reach the insular cortex, but none seemed to terminate within the claustrum. Predominantly, the fibers carried in the extreme capsule were cortical association fibers. However, some fibers traversed the claustrum to join the external capsule directly; others entered it behind the lenticular nucleus.

Along the length of the lesions, fibers were distributed from the frontal lobe into the external capsule. From this capsule, a few extremely fine fibers coursed medially into the putamen, but could not be traced for any great distance. The majority of the fibers passed caudally, supplemented by other fibers from the corona radiata along their course. Many worked their way ventrally and were joined by fibers of the extreme capsule when the capsules became continuous posteriorly. Thus, the fibers ran medially and ventromedially, sublenticularly or postlenticularly, passing over the capsule of the lateral geniculate nucleus (fig. 17) into the tegmentum where they projected directly into the red

nucleus and the surrounding tegmental gray. A few fine fibers were traced into the substantia nigra.

Degenerated fibers from the lesion in the motor cortex entered the internal capsule. These were indicated by extremely coarse Marchi granules which continued in the corticospinal tract. Destruction in the left medullary pyramid was very marked in comparison to the amount of degeneration within the contralateral pyramid (fig. 18).

Protocol for monkey 2

A 5.2-kg healthy male macaque was subjected to a frontal craniectomy. The dura was reflected and the arcuate and principal fissures exposed. Using a scalpel, a lesion was made directly above the caudal end of the principal fissure and this lesion was enlarged with a surgical aspirator to involve the rostral margin of the arcuate fissure (fig. 2).

A second dural opening was made at the rostral end of the lateral fissure. With a surgical aspirator, area 11 (Mettler, '47) at the ventral border of the lateral surface of the brain was ablated. The wound was closed in the usual manner.

These procedures were tolerated extremely well. The animal displayed no signs of infection or other sequelae. Nine days later, a left dorsal spinocerebellar tractotomy at the second cervical level was performed by another observer (Vachand, '59) which caused some hypotonicity and weakness of the left lower extremity.

Two weeks after the tractotomy, the animal was sacrificed and perfused and the brain removed. Gross examination revealed two left-sided lesions. The more dorsal lesion, triangular in outline, was located dorsal to the principal fissure and rostral to the arcuate fissure. The second lesions destroyed area 11 (Mettler, '47).

Microscopic examination revealed a destruction of a portion of the inferior frontal gyrus, involving superficial cortex and extending into the white matter, at most about 1.5 cm. The lesion in area 8 destroyed superficial cortex and involved the underlying white matter.

Marchi granules were traced in serial sections from the lesion in area 11 into the corona radiata and spread as diffuse, me-

dium-sized and fine granules, into the frontal lobe. They also could be followed, by way of the corpus callosum, into corresponding regions of the opposite hemisphere. Degenerated fibers from the left-sided lesion of area 8, joined and intermingled with those from area 11. Degenerated fascicles coursed from one frontal lobe through the corpus callosum to corresponding regions of the opposite hemisphere.

A very few fibers were traced from the subcallosal bundle, from the anterior limb of the internal capsule, and from the corona radiata into the caudate nucleus, ipsilaterally, where they appeared to terminate in the caudate nucleus. Degenerated fibers also passed into the anterior limb of the internal capsule and the common external and extreme capsules on the side of the injury and, after decussation through the corpus callosum, to the corresponding capsules in the contralateral hemisphere.

On each side of the brain, from the anterior limb of the internal capsule, a few fibers entered the putamen. Here some fibers terminated and some continued medially into the globus pallidus to join other fascicles from the internal capsule. Degenerated fascicles were traced through the lenticular fasciculus to the zona incerta and the nucleus of the field of Forel. Here part of these fibers ended, but others continued caudalward to discharge into the red nucleus. From the putamen certain more ventral bundles passed into the ansa lenticularis to discharge to the nucleus of the field of Forel or continued directly into the lateral and the ventrolateral regions of the tegmentum around the red nucleus. Joining this system were fibers which passed from the corona radiata and the internal capsule into, and through the edge of, or across the lateral thalamic nucleus to the lateral and ventrolateral tegmental areas. A few fibers distributed to the substantia nigra.

Degeneration granules from both lesions were present in the region of continuity of the external and the extreme capsules. From the extreme capsule, cortical association fibers distributed to the superior, the middle, the inferior temporal, and the hippocampal gyri. A very few gran-

ules were traced from the extreme capsule into the insular cortex. These were very delicate and could not be followed over any great distance. From the external capsule, a few fine fibers were added to the extreme capsule after passing through the dorsal claustrum. None appeared to terminate within the claustrum. The fibers carried in the extreme capsule were mostly cortical association fibers connecting frontal with temporal lobes.

From the lesions, degenerated fibers were also distributed through the corona radiata into the external capsule. Most of these fibers coursed within the capsule but a few fine fibers appeared to pass medially into the putamen. These could not be traced for any great distance due to the delicacy of their medullation. The fibers within the external capsule (fig. 19) collected in a bundle and passed ventrally, beneath the anterior commissure, toward the base of the brain (fig. 21) where a few fibers entered the diagonal band of Broca. The remainder of the fibers coursed medially and then dorsally to enter the ansa lenticularis (fig. 13). Beneath the lenticular nucleus they joined fascicles from the basal ganglia also turning into the ansa lenticularis. The fibers that had run beneath the anterior commissure were distinct from those of the ansa, as the latter bundle joined the lenticular fasciculus in the zona incerta and the field of Forel. However, in the field of Forel, the fibers intermingled and became inseparable. It is uncertain whether the degenerated fibers in the ansa ended in the nucleus of the field of Forel or whether they were discharged into the red nucleus and the tegmentum around the red nucleus. A very few fibers remained in the external capsule and worked their way caudoventrally into the inferior longitudinal fasciculus. These remaining fibers were joined by degenerated fibers coming into this region from the extreme capsule to pass medialward beneath the ventral claustrum. As the external and the extreme capsules became confluent posteriorly, some of the degenerated fibers from the two capsules intermingled. They coursed medially, sublenticularly, or postlenticularly, to pass over the capsule of the lateral geniculate nucleus and to project into the lateral and

ventrolateral tegmentum of the midbrain together with the corticotegmental fibers which had descended in the posterior limb of the internal capsule. Some of the fibers in the corona radiata continued caudally to parietal levels. They then turned into the dorsal part of the external capsule, passing obliquely medialward through the caudal end of the lenticular nucleus to reach the posterior limb of the internal capsule. Here they intermingled with corticopontine and corticotegmental fibers in the posterior limb of the internal capsule so that their ultimate termination could not be ascertained.

Protocol for monkey 3

A left frontal craniectomy was done on a 5.10 kg male macaque which had undergone a left spinocerebellar tractotomy at C₂ (Vachananda, '59) one week earlier. Reflection of the dura permitted identification of the arcuate and the principal fissures. Two lesions were made, one above and one below the superior limb of the left arcuate fissures. The inferior portion of the central fissure was exposed through a second opening in the dura and the sensory cortex immediately caudal to this fissure was ablated.

The animal tolerated these operative procedures extremely well. No changes in behavior or neurological deficits resulted from the brain operation. After two weeks, the animal was sacrificed and perfused in the usual fashion. On gross examination, the brain showed two frontal lobe lesions in the region of the arcuate fissure (fig. 3). These lesions were almost continuous and seemed to involve both surface cortex and the underlying white matter. A parietal lobe lesion occupying the lower portion of the sensory cortex about two centimeters above the lateral fissure was also noted (fig. 3).

Microscopic examination revealed two left frontal lobe lesions, above and below the arcuate fissures. These involved the superficial cortex on the dorsolateral surface of the brain and extended into the underlying white matter. A diffuse, fine degeneration spread into the corona radiata and throughout the frontal cortex at the level of these lesions, and extended, by way of the corpus callosum, into the cor-

responding regions of the opposite hemisphere. A few degeneration granules were seen in the frontal regions of the hemisphere, on the side opposite the injury, but were extremely delicate and could not be followed for any considerable distance.

A few fibers entered the subcallosal bundle and the cingulum of the left side. No degenerated fibers were seen in the caudate nucleus. However, some medium and fine degenerated fascicles passed from the anterior limb of the internal capsule into the putamen (fig. 22). Here some fibers terminated, but a few continued their course medially into the globus pallidus where other fibers from the internal capsule were added. Certain of these combined fascicles coursed dorsally in the lenticular fasciculus (fig. 20), through the zona incerta and the field of Forel, to end on the nucleus of this field. Others discharged directly into the red nucleus. Ventrally, fibers were seen entering the ansa lenticularis, to pass, in part, to the ventrolateral and the lateral tegmental areas around the red nucleus. To this system were added corticotegmental fibers from the internal capsule and still other corticotegmental bundles from the area of the lesions which traversed the internal capsule and turned medially through the lateral thalamic nuclei and the nucleus ventralis posterior pars lateralis to reach the red nucleus and the ventrolateral and the lateral tegmental regions around this nucleus.

Degenerated fascicles, present in the left corona radiata, were followed into the rostral continuity of the extreme and the external capsules. In the extreme capsule, fine Marchi granules indicated fascicles traveling ventralward and caudoventralward to distribute to the superior and the middle temporal gyri. Some fibers also coursed to the inferior temporal and hippocampal gyri. These cortical association fibers were joined by a few fine degenerated fibers passing across the dorsal claustrum from the external to the extreme capsule. Whether any termination occurred in the claustrum could not be determined. Little evidence for association fibers connecting the frontal lobe with the insular cortex was present. The components of the ex-

treme capsule seemed to be primarily cortical association fibers.

At the rostral border of the lesion, fibers were distributed from the frontal lobe into the external capsule (fig. 24). For the most part, these fibers traveled ventrally and caudoventrally within their capsular boundary to appear as clusters of fascicles just dorsal to the anterior commissure at the level of its decussation. Here the degenerated fascicles turned medially, paralleling the anterior commissure, to enter the ventral portion of the putamen, and then pass into the globus pallidus behind the decussation of the anterior commissure. In their course they were joined by other fibers from the globus pallidus. The common bundle continued toward the ansa lenticularis where the fibers intermingled and became inseparable. Some fibers continued their course into the base of the hemisphere entering the diagonal band of Broca. Other fibers from the ansa lenticularis joined the fibers of the lenticular fasciculus in the region of the nucleus of the field of Forel. Some fascicles of both bundles ended in this nucleus; others projected into the red nucleus and the ventrolateral and the lateral tegmental area around this nucleus. A few fine fibers remained in the ventral part of the external capsule. These fibers maintained their position until they reached the posterior part of the lenticular nucleus. Here they turned medially, postlenticularly or sublenticularly, to join with fibers from the inferior longitudinal bundle. The combined fiber bundle passed over the capsule of the lateral geniculate nucleus to discharge into the red nucleus and the lateral and ventrolateral portions of the tegmentum.

The lesion of the left parietal hemisphere involved a portion of the sensory cortex at a position approximately two centimeters above the lateral fissure. This lesion was superficial, destroying surface cortex without direct injury to the underlying white matter. Degenerated fibers, by the way of the corpus callosum, traveled into the corona radiata of the opposite hemisphere to intermingle with commissural fibers from the frontal lesions. Coarse and medium-sized granules could be traced into the posterior limb of the internal capsule and into the extreme capsule. Within

the latter, degenerated cortical association fibers to the temporal lobe were noted. Few if any granules were found in the external capsule.

Some degenerated fibers from the sensory cortex were evident in the posterior limb of the internal capsule on the side of the lesion. A few of these fibers turned into the putamen; some entered the globus pallidus, the lenticular fasciculus, and the ansa lenticularis. These probably also distributed to the red nucleus and the lateral and the ventrolateral tegmentum around and caudal to the red nucleus. At the caudal end of the lenticular nucleus, fibers passed into the external capsule. Such fascicles seemed to aggregate at parietal levels and passed obliquely ventromedialward across the putamen into the posterior limb of the internal capsule. To this system were added degenerated corticotegmental fibers from the posterior limb of the internal capsule and still other corticotegmental fibers which had turned through the posterior part of the thalamus to reach the red nucleus and the tegmental areas lateral and ventrolateral to it.

A few fine, diffuse corticospinal and corticopontine fibers were traced from the level of the parietal lesion through the posterior limb of the internal capsule and the base of the brain stem. They were indicated by a few medium-sized or coarse Marchi granules.

Protocol for monkey 4

A left frontal craniectomy was performed on a 7.2 kg male macaque, the dura was reflected and a cortical lesion was made in area 11 (Mettler, '47). Frequent observations during the next two weeks showed no impairment of motor function and no change in behavior. No other physical or neurological defects were noted.

Two weeks after the operation, the animal was sacrificed and perfused and the brain removed. On gross examination, a left frontal lesion at the rostral end of the left arcuate fissure was noted (fig. 4). The destruction involved the base of the arcuate fissure and extended dorsally and rostrally for approximately 1.5 cm. Involvement of the superficial cortex and the underlying white matter was found.

Microscopic examination revealed a left frontal lesion involving area 11, which destroyed the anterior borders of both the frontal and the temporal opercula and the rostral portion of the insular cortex. A medium to fine granular degeneration was traced from the tip of the frontal operculum into the corona radiata, the anterior limb of the internal capsule, and the cortical association bundles as far as the middle and the superior frontal gyri at the level of the lesion. A few degenerated commissural fibers were followed into the contralateral cingulate gyrus and, by way of the contralateral corona radiata, to the superior, the middle, and the inferior frontal gyri, and into the anterior limb of the internal capsule of the opposite hemisphere.

From the rostrum of the corpus callosum, from the subcallosal bundle, and from the internal capsule, a few fibers passed into the caudate nucleus on the side of the lesion. They continued through the anterior limb of the internal capsule and, by way of the gray bridges, to the putamen. These fibers in the putamen were augmented by fascicles from the internal capsule and the corona radiata which turned into the putamen of each hemisphere. Here some fibers synapsed, but others continued medially into the globus pallidus, and, through it, into the lenticular fasciculus and ansa lenticularis to discharge directly into the red nucleus and the lateral and ventrolateral tegmentum around this nucleus. Joining this system were corticotegmental fibers which continued from the corona radiata into the internal capsule to course near the edge of the lateral thalamic nucleus and across nucleus ventralis posterior pars lateralis to reach the red nucleus and the lateral and ventrolateral tegmentum around this nucleus. Corticotegmental fibers from the inferior frontal gyrus were also carried in the internal capsule to the red nucleus and to the lateral and the ventrolateral tegmentum around its capsule.

From the frontal lesion degenerated fibers, after a partial decussation, entered the common external and extreme capsules bilaterally. Some cortical association fibers were distributed through the extreme capsule to the insular cortex, others passed

ventrally in this capsule, into the superior, the middle, and the inferior temporal and the hippocampal gyri. The fibers that entered the extreme capsule were predominantly cortical association fibers, but some fibers appeared to traverse the dorsal claustrum, a few at a time, to enter the external capsule.

Marchi granules indicated degenerated fibers extending from the insular cortex into the extreme capsule (fig. 25). These were chiefly cortical association fibers connecting frontal and insular cortices with superior, middle, and inferior temporal and hippocampal gyri. Coarse granules indicated the presence of fascicles from the insular cortex through the extreme capsule, the dorsal claustrum, and the external capsule to the lateral margin of the putamen. They could be traced for no great distance within the putamen. Other fibers were traced dorsally through the extreme capsule and across the dorsal claustrum into the white matter of the frontal lobe near the anterior limb of the internal capsule.

Medium and coarse granules indicated degenerated fibers from the superior temporal gyrus to the middle temporal gyrus. Similar fibers passed to the inferior temporal and the hippocampal gyri. Many such fibers were traced to the extreme capsule and through it to the inferior frontal gyrus. Others were carried in the extreme capsule, but passed dorsomedially through the dorsal claustrum into the corona radiata. Medium-sized and large degenerating fibers were traced from the temporal operculum through the extreme capsule and dorsal claustrum into the external capsule. A few fibers traveled still more medially to reach the ventrolateral margin of the putamen. These could not be followed for any great distance nor could fibers be found ending within the claustrum. No degeneration was seen either in the ventral claustrum or in the amygdala.

Cortical association fibers from the inferior frontal gyrus, the insula and the superior temporal gyrus entered the extreme capsule on the side of their origin or decussated to the other side. Some of the crossing fibers reached the extreme capsule on the contralateral side and continued caudoventrally in it. Bilaterally,

then, at the posterior end of the putamen, these fibers collected and joined fibers of the external capsule passing over the capsule of the lateral geniculate nucleus. Both groups of fibers projected directly into the red nucleus and the lateral and ventrolateral tegmentum around it.

Fibers from the frontal cortex, the insula, and the temporal operculum were distributed into the external capsule. A few of these fibers passed medialward into the lateral margin of the putamen, but the majority of them were contained within the capsular boundary passing caudovertrally until they were joined postlenticularly by fibers in the extreme capsule. Other degenerated fibers continued into the lateral border of the putamen but could not be followed very far due to their delicate medullation.

From the lesion in the superior temporal gyrus, degenerated cortical association fibers turned ventrally into the middle temporal gyrus. Connections with the inferior temporal and hippocampal gyri were also noted. Due to the extensiveness of the island lesion anteriorly (which included the external and extreme capsules as well as the temporal operculum) the origin of fibers turning into the external and extreme capsules could not be determined. However, contributions from the temporal lobe were traced into both the external and the extreme capsules posteriorly. Degenerating fascicles from the superior and the middle temporal gyri crossed through the anterior commissure to distribute to the uncinata fasciculus, the inferior temporal gyrus and the hippocampal gyrus of the opposite hemisphere. No fibers were traced into the external capsule or to the ventral claustrum of the right side.

From the left frontal operculum, fibers entered the anterior limb of the internal capsule on the side of the lesion and distributed, by way of the corpus callosum, to the contralateral internal capsule. Bilaterally, these degenerated fibers in the internal capsule turned ventrally into the globus pallidus. To this system were added fibers from the external capsule and the corona radiata which coursed medialward to reach the globus pallidus. Here some fibers ended; others continued through the lenticular fasciculus to the zona incerta

and the nucleus of the field of Forel, where, after some synapse, they discharged into the red nucleus.

Microscopic examination of the left hemisphere showed destruction of the frontal and the temporal opercula as well as of the insular cortex. The lesion extended medially to involve the extreme capsule, the ventral claustrum, the external capsule, and the ventrolateral margin of the putamen. A ventral extension of the lesion involved the superior temporal gyrus and the lateral part of the middle temporal gyrus. From the left inferior frontal gyrus degenerating fibers were traced into the corona radiata and throughout the white matter of the superior and the middle frontal gyri. Fine Marchi granules were followed into the anterior limb of the internal capsule and into the cingulate gyrus. Degenerated commissural fibers passed into the corpus callosum to distribute contralaterally to the cingulate gyrus, throughout the frontal lobe at the level of the lesion, and into the anterior limb of the internal capsule. No Marchi granules were found in the caudate nuclei. Fibers from the frontal operculum coursed into the junction of the external and the extreme capsules rostrally and into both the external and the extreme capsules as they became separated more posteriorly.

Degenerated fibers from the insular cortex were followed into the extreme capsule (fig. 25). Some fibers radiated dorsally toward the frontal lobe, others coursed ventrally in the extreme capsule toward the temporal cortex. Coarse and medium-sized degenerated fascicles from the island extended medially through the extreme capsule and the dorsal claustrum into the external capsule. Whether any synapse occurred in the claustrum itself could not be determined. A few fine fibers coursed medialward in the combined external and extreme capsules to reach the posterior limb of the internal capsule (fig. 26). Other fibers turned ventrally and passed obliquely, postlenticularly or sublenticularly, over the capsule of the lateral geniculate nucleus to join corticotegmental fibers carried in the internal capsule and corticotegmental fibers passing through the nucleus lateralis and the nucleus ventralis posterior pars lateralis of the

dorsal thalamus. Still other corticotegmental fibers in the ansa lenticularis were added to the common paths which discharged to the lateral and ventrolateral tegmentum around the red nucleus. A few corticonigral fibers were traced to the substantia nigra.

Degenerated fascicles were traced from the inferior frontal gyrus into the corpus callosum to reach the midline septal nuclei. Some of these were followed into the fornix system. Fibers from the external capsule, the internal capsule, and the superior temporal gyrus passed into the anterior commissure to distribute to the opposite hemisphere.

Protocol for monkey 5

Following a left frontotemporal craniectomy, the dura was reflected, the temporal operculum partly ablated, and the insular cortex exposed in a 3-kg female macaque. During the proceeding, a hemorrhage occurred in the insular region, which necessitated packing the area with gelfoam so that further manipulation was considered inadvisable.

Two weeks later a right frontal craniectomy was carried out, the dura opened, and the central fissure exposed. Stimulation of the region just rostral to this fissure on the lateral hemisphere wall produced movements of the contralateral upper extremity. A lesion was made in this "arm" area with a surgical aspirator.

Following the experimental injury the animal showed an unwillingness to use her left upper extremity and carried this limb in a peculiar position of extension at the wrist and elbow. The tonus appeared to be the same in the two upper extremities.

When the brain was removed, following sacrifice and perfusion of the animal, a right frontal lesion involving area 4 on the lateral surface posterior to the middle third of the arcuate fissure was noted (fig. 5). On the left side, removal of a portion of the frontal and the temporal opercula had been accomplished and there was a lesion in the insula (fig. 6).

The extreme capsule contained degenerated fibers from the frontal operculum, from the insular cortex (fig. 27) and from the superior and the middle temporal gyri. These were predominantly association fi-

bers interconnecting the injured cortical regions. A few fine fibers passed from the extreme capsule to the dorsal claustrum and into the external capsule. Whether any of these fibers ended within the claustrum could not be determined, due to their paucity and delicate myelination. Other fibers remained within the extreme capsule coursing caudoventrally within the capsular boundary to join fibers in the external capsule as the capsules became confluent at the caudal end of the lenticular nucleus. These were projected as a common bundle into the dorsolateral and lateral tegmentum around the red nucleus.

Fibers from the inferior frontal gyrus, from insular cortex (which traversed the extreme capsule and dorsal claustrum), and from the superior and the middle temporal gyri entered the external capsule (fig. 27). A few extremely fine fibers coursed medially into the putamen where they were seen at the lateral margin. Some fibers interconnected the island with the frontal cortex but the great majority of the fascicles passed posteriorly in the external capsule. The more dorsal fibers swung ventromedialward behind the lenticular nucleus; the others turned postlenticularly or sublenticularly to join fibers in the posterior limb of the internal capsule. Together, as a common bundle, the fibers were projected over the capsule of the lateral geniculate nucleus (fig. 29) into the lateral and dorsolateral tegmentum around the red nucleus where they came into association with corticotegmental fibers which traversed the nucleus lateralis and nucleus ventralis posterior pars lateralis of the dorsal thalamus. Some of these fibers entered the pons with the corticopontine fibers from the anterior limb of the internal capsule. This corticopontine system originated in the frontal operculum. A few fine fibers were traced into the substantia nigra.

Corticotegmental fibers of many origins and by several pathways were thus projected into the lateral and the dorsolateral tegmentum around the red nucleus. Fibers that traveled by way of the basal ganglia (fig. 28), fibers from the posterior limb of the internal capsule, fibers through the nucleus lateralis and nucleus ventralis posterior of the dorsal thalamus, and fas-

cicles that traversed the extreme and the external capsules all converged to a common termination in the red nucleus and the lateral and the dorsolateral tegmentum around this nucleus.

Microscopically, the lesion on the right side involved the dorsolateral portion of area 4. A coarse granular degeneration extended into the corona radiata and distributed into the dorsomedial portion of the superior frontal gyrus as well as to the middle and the inferior frontal gyri. A few degenerated fibers entered the dorsal part of the external capsule. No connection with the extreme capsule was noted. Commissural fibers were traced into the corpus callosum, passing through the corona radiata to the superior frontal gyrus and the internal capsule of the opposite hemisphere. From the ipsilateral internal capsule, a few coarse fibers were followed into the globus pallidus. These fibers lost their heavy medullated sheaths, and whether they terminated in the globus pallidus or continued into the lenticular fasciculus to reach the red nucleus could not be determined. Some coarse fibers extended into the dorsal thalamus and passed through the nucleus lateralis and the nucleus ventralis posterior pars lateralis to the dorsolateral and the lateral portions of midbrain tegmentum near the red nucleus. The great majority of fibers traveled as a dense bundle in the genu and the posterior limb of the internal capsule as the corticospinal tract, passing through the pes pedunculi and the base of the pons to form the pyramid. Some coarse granulation indicated degenerated heavily medullated fibers, which were traced through the corpus callosum to reach the contralateral internal capsule and then were followed down through the brainstem into the pyramid at medulla levels.

Protocol for monkey 6

A left frontotemporal craniectomy was carried out on a 3.7-kg female macaque. After the dura was reflected, the arcuate and the principal fissures were identified and a considerable portion of area 8 (fig. 7) dorsal to the principal fissure and rostral to the arcuate fissure was ablated. A second lesion was placed in the temporal operculum (fig. 8).

The animal had a stormy postoperative course due to rhinorrhea and difficult respiration. No impairment of motor function or neurologic change in behavior was noted up until the time she was sacrificed and perfused about two weeks after the experiment.

Microscopic examination revealed a lesion of the left middle frontal gyrus involving the superficial cortex and extending into the underlying white matter. A left temporal lesion destroying the rostral portion of the temporal operculum was also noted.

Marchi granules from the middle frontal gyrus spread diffusely into the white matter, through the corona radiata, and into the superior and the inferior frontal gyri. Degenerated commissural fibers traveled, by way of the corpus callosum, into the corresponding regions of the opposite hemisphere. Degenerated fibers were followed also into the internal capsule and the common external and extreme capsule bilaterally. An exceedingly few fibers from the subcallosal bundle and from the surrounding white matter entered the head of the caudate nucleus bilaterally and spread throughout it. Possibly some fibers terminated; a few passed into the putamen through the anterior limb of the internal capsule by way of the gray bridges. Most of the degenerated fibers from the frontal lesion passed ventralward, medial to the anterior limb of the internal capsule, directly into the putamen. Some of these fibers continued to the base of the hemisphere into the diagonal band of Broca beneath the anterior commissure. A few reached nucleus accumbens. A few medium and fine Marchi granules were traced from the anterior limb of the internal capsule into the putamen. A small number of degenerated fibers appeared medially in the globus pallidus where they were joined by other fibers from the internal capsule. Some degenerated fibers were followed from the globus pallidus into the ansa lenticularis; a few such fibers from the base of the hemisphere also turned dorsally into the ansa lenticularis. Neither of these contributions was large. Other degenerated fascicles were followed, however, into the lenticular fasciculus, to the zona incerta, and to the nucleus of the

field of Forel where some ended. Other small fascicles continued to discharge into the red nucleus, the tegmentum dorso-lateral, lateral and ventral to it, the nucleus of Darkschewitsch, and the oculomotor nucleus (entering its lateral side). Still other degenerated fibers traveled along the ansa to reach the region behind the red nucleus. Some fibers (and a few delicate fascicles from the internal capsule) turned medialward into and through the nucleus ventralis posterior pars lateralis to course to the red nucleus and the surrounding tegmentum. Scattered Marchi granules were found in the substantia nigra.

Marchi granules indicated that degenerated fascicles passed from the left frontal cortex into the common external and extreme capsule rostrally on each side of the brain, those to the right hemisphere having crossed through the corpus callosum. When the external and the extreme capsules became separated, some degeneration was seen in each. Fewer degenerated fibers were seen on the contralateral side than on the side of the lesion. In the extreme capsule, medium and fine degenerated fibers were scattered ventrally and caudoventrally toward the temporal lobe. In the superior temporal gyrus, they were augmented by fascicles extending from the lesion in the left temporal operculum. Together the degenerated bundles traveled to the middle and the inferior temporal gyri. A few fibers passed to the hippocampal gyrus. The cortical association fibers in the extreme capsule were joined by fibers passing from the external capsule through the dorsal claustrum. Whether any of these terminated in the claustrum could not be determined. Little evidence of connections with insular cortex was found. The components of the extreme capsule are cortical association fibers.

In the most rostral sections, a few degenerating fibers were noted in the external capsule. These coursed laterally through the dorsal claustrum and entered the extreme capsule as cortical association fibers. No contribution to the putamen from the external capsule was seen.

From the frontal lesion, fibers entered the anterior limb of the internal capsule directly to become corticobulbar fibers. Others coursed in the association bundles

of the corona radiata, and turned into the internal capsule at more caudal levels. Some fibers accumulated in the corona radiata at parietal levels and passed directly into the posterior limb of the internal capsule. A few entered the external capsule at the posterior end of the lenticular nucleus and traveled obliquely ventromedially across the dorsal part of the putamen to reach the internal capsule. From many areas fibers were traced through the internal capsule. Some fibers of the internal capsule turned off to the putamen and the globus pallidus bilaterally. Others turned medially through the nucleus lateralis and the nucleus ventralis posterior pars lateralis to enter the red nucleus and the dorsolateral, the ventral and the lateral areas of the tegmentum adjacent to it. Joining this system were corticotegmental fibers carried in the posterior limb of the internal capsule which discharged directly into the tegmentum of the midbrain. Corticobulbar fibers in the internal capsule entered the oculomotor nucleus ventrally to continue caudal to it. A few frontopontine fibers were noted.

Marchi granules in the region of the lesion in the left temporal operculum were also identified in serial sections. A few medium and fine fibers traveled into the extreme capsule. These were quite diffuse and could not be traced for any considerable distance within this capsule. No fibers passed into the insular cortex. This lesion was extremely small, however, and the degenerated fibers were very few and quite diffuse, making this series quite unsatisfactory for determining connections of the temporal lobe with the frontal or the insular cortices. However, a few fibers spread from the lesion into the middle and the inferior temporal gyri and the hippocampal gyrus. Some Marchi granules were found in the inferior longitudinal bundle; a few Marchi-stained fibers traveled beneath the ventral claustrum to the ventral part of the external capsule. No degeneration was seen in the ventral claustrum, however. The degenerated fibers in the inferior longitudinal bundle and in the ventral part of the external capsule maintained their position in serial sections until they reached the posterior part of the putamen. Here, as a few diffuse fibers, they

turned medialward, postlenticularly or sublenticularly, over the capsule of the lateral geniculate nucleus to reach the usual mid-brain areas. A few fibers entered the substantia nigra. A few temporopontine fibers were also identified.

Protocol for monkey 7

A temporal craniectomy was performed on a 3.1-kg female macaque, the dura reflected and ablation of left area 22 (fig. 9) accomplished with a surgical aspirator. The animal showed no ill effects from the experiment during the next 10 days. At the end of this period, a similar operation was carried out in the opposite hemisphere. During the succeeding two weeks, the animal showed no demonstrable defects. Then, she was sacrificed and perfused and the brain removed and prepared for study by the Marchi technique.

Post mortem examination of the brain showed bilateral lesions of the posterior portion of each temporal operculum. The lesion in right area 22 (fig. 10) was slightly deeper than that in area 22 on the left.

Microscopic observation revealed bilateral destruction of a portion of the temporal operculum. The lesion on the right side involved the base of the island and transected the extreme capsule and the lateral third of the ventral claustrum. The left-sided lesion involved superficial temporal opercular cortex and the underlying white matter. Injury to the edges of both left and right parietal opercula were noted. The lesions were essentially the same on the two sides so the paths on the left side only are reported.

Fibers from the temporal operculum were traced into the extreme capsule. Some continued dorsally within the capsule to distribute to the parietal operculum. Other cortical association fibers coursed ventrally into the middle and the inferior temporal gyri and into the hippocampal gyrus. A few fine fibers passed through the extreme capsule into the dorsal claustrum and through this area into the external capsule. Whether any fibers terminated within the claustrum could not be determined. A few fine fibers connected the superior temporal gyrus with the insular cortex.

Due to the involvement of the tip of the parietal operculum, Marchi granules were present in the extreme capsule, the dorsal claustrum, and the external capsule. The degenerated fibers represented by these granules also entered the corona radiata to spread throughout the parietal lobe and into the posterior limb of the internal capsule. Commissural fibers, by way of the corpus callosum, projected impulses to corresponding areas of the two sides due to the bilaterality of the lesions. A few fibers were traced to the cingulate gyrus on both sides. Several fine fascicles from the subcallosal bundle passed into the head of the caudate nucleus and into the putamen through the gray bridges. From the corona radiata, from the posterior limb of the internal capsule, and from the external capsule, fibers coursed into the putamen and, through it, into the globus pallidus, beyond which some fibers could not be traced. Other fascicles entered the globus pallidus from the internal capsule and continued through the lenticular fasciculus and the ansa lenticularis to the red nucleus and the tegmentum lateral to it. To this system were added fibers from the posterior limb of the internal capsule and the corona radiata, traversing the nucleus lateralis and the nucleus ventralis posterior pars lateralis of the dorsal thalamus. All these ended in the red nucleus and the tegmental areas surrounding the capsule of this nucleus.

Most of the fibers carried in the extreme capsules were cortical association fibers. They arose in parietal and temporal opercula and interconnected parietal, insular, and temporal cortices. Some fine fibers remained in the extreme capsule working their way caudoventrally to join fibers in the external capsule. These various fibers extended dorsal to and then medial to the lateral geniculate nucleus to enter the tegmentum lateral to the red nucleus.

In the external capsule were fibers from parietal operculum and contributions from the superior temporal gyrus which passed through the dorsal claustrum. A few fine fibers were traced into the putamen. These were extremely delicate and could not be followed for any considerable distance. However, the majority of fibers remained within the external capsule as the extreme

and external capsules became confluent behind the putamen. Here the degeneration granules from the external capsule passed obliquely behind the lenticular nucleus to join corticotegmental and corticopontine fibers in the posterior limb of the internal capsule. As the external and extreme capsules united ventrally, other fibers from the temporal lesions in the operculum accumulated in a bundle which coursed postlenticularly and then sublenticularly over the capsule of the lateral geniculate nucleus directly into the red nucleus and the midbrain tegmentum. Some of these fibers from the posterior aspect of the superior temporal gyrus were projected as corticopontine fibers. A few fibers were traced to the substantia nigra.

Protocol for monkey 8

The anterior portion of area 7 was destroyed in a 4.8-kg female macaque (fig. 11). No evidences of the injury were seen during the next two weeks. At the end of the period the animal was sacrificed and perfused and the brain removed and prepared for microscopic study.

Microscopic examination showed destruction of the parietal cortex on the dorsolateral surface, corresponding to area 7. This lesion involved also the underlying white matter. Many diffuse, medium-sized to fine granules were present throughout the parietal lobe at the level of the lesion and in the white matter of the temporal lobe, the fusiform and the lingual gyri, and the sagittal stratum. Degenerated fascicles were present in the white matter beneath the posterior part of the insula. A few fibers entered the insular cortex, but the majority of the cortical association fibers connected the parietal with the temporal lobe. Some Marchi granules were also found in the tapetum, the alveus, the gyrus fornicatus, and the lingual gyrus. Numerous degenerated fibers from the left corona radiata passed into the splenium of the corpus callosum. They connected the corresponding regions of the two hemispheres. Fibers distributed to the lateral and caudal part of the pulvinar bilaterally, some fascicles having crossed in the corpus callosum. Some of the fibers ended in the pulvinar but others coursed through the pulvinar (fig. 30) to enter the

superior colliculus as corticotectal fibers. In the tectum a few fibers crossed in the commissure of the superior colliculus.

Numerous degenerating association fibers extended anteriorly in the superior longitudinal fasciculus to connect the parietal with the frontal lobe. Fibers were traced from this region into the cingulum and to the cingulate gyrus, bilaterally. Commissural fibers passed into the corpus callosum at almost all levels. Coarse, medium-sized, and fine Marchi granules were found in the corona radiata and in the posterior limb of the internal capsule. The degenerated fibers turned medialward into and through the nucleus lateralis and the nucleus ventralis posterior pars lateralis to discharge to the zona incerta, the red nucleus and the dorsolateral, lateral, and ventrolateral tegmental areas around the red nucleus. Some of these fibers crossed in the tegmentum of the midbrain. In the posterior limb of the internal capsule were also parietopontine fibers, which passed into the pes pedunculi and entered the pons.

Fibers from the corona radiata entered the anterior limb of the internal capsule at frontal lobe levels. A few fibers entered the putamen. Here some of them could be followed no farther, but other fibers coursed medially into the globus pallidus where many more fascicles were added from the internal capsule. Fine degeneration granules were seen ventrally in the ansa lenticularis and could be traced along fiber bundles projecting into the lateral, the dorsolateral, and the ventrolateral tegmental areas of the midbrain. Degenerated fibers in the globus pallidus turned dorsally to enter the lenticular fasciculus, the zona incerta, the nucleus of the field of Forel and ultimately the red nucleus. To this system were added corticotegmental fibers that discharged directly into the tegmentum. These were carried in the internal capsule. Similar discharge paths were found in the other hemisphere.

Cortical association fibers from the parietal lesion could be followed to the more caudal portions of the temporal lobe. These were traced rostrally in the inferior longitudinal fasciculus where they collected at the caudal end of the lenticular nucleus. Some of these fibers were traced medialward, then postlenticularly or sub-

lenticularly over the capsule of the lateral geniculate nucleus to the tegmental areas, including the red nucleus.

A few fibers joined the corticopontine fibers in the posterior limb of the internal capsule as a contribution to this system from the temporal lobe. No Marchi degeneration granules were seen in the external capsule, the claustrum, or the extreme capsule.

Protocol for monkey 9

A left parieto-occipital skin incision was made, the parietal bone rongeuired and the underlying dura reflected in a 5.5-kg healthy male macaque. The dorsal portion of area 19 and a small portion of the adjoining area 18 were ablated (fig. 12). No motor defects were noted following this lesion.

After two weeks, following the usual procedure, the brain was removed and examined grossly. A left preoccipital lesion involving the superficial cortex and the underlying white matter of the dorsal portion of area 19 was seen. A right-sided destruction of surface cortex behind the central part of the sensory cortex was also evident. Coronal sections were made and the brain was stained using the Marchi method.

Microscopic examination of the brain revealed a destruction of the left preoccipital cortex in the dorsal portion of area 19. This lesion involved the underlying white matter and spread throughout the adjoining areas. Diffuse, medium and fine granules were present in the sagittal strata. Association fibers connected the parietal with the temporal lobe, coursing into the fusiform and the lingual gyri. A few fine fibers were noted in the white matter beneath the posterior part of the insula. Some granules were seen also in the tapetum, the alveus, the gyrus fornicatus, and the lingual gyrus. Degeneration from the parietal lesion of right area 5 was seen. However, the preparations were unsatisfactory for a study of the cortical projection systems. Commissural fibers passed into the splenium of the corpus callosum and intermingled with degenerated fascicles from the lesion on the left side. The terminations of these commissural fibers could not be determined. Fibers entered

the lateral and the caudal parts of the pulvinar before and after decussation. This relation was much more pronounced on the left side, however. Here some fibers entered, but others continued into the superior colliculus (especially on the left side) as corticotectal fibers. Within the tectum, a few fibers crossed in the commissure of the superior colliculus. Some degenerated fascicles coursed directly into the tegmentum of the midbrain, as corticotegmental fibers.

In the inferior longitudinal fasciculus were cortical association fibers that could be traced from the preoccipital area to the temporal lobes of both hemispheres, a partial decussation occurring through the corpus callosum. A very few fibers coursed medially, postlenticularly or sublenticularly, over the capsule of the lateral geniculate nucleus to reach the red nucleus and the midbrain tegmentum.

Some cortical association fibers also traveled anteriorly in the superior longitudinal fasciculus, connecting the parietal with the frontal lobe. Crossed fascicles reached the contralateral frontal area. From the corona radiata, fibers entered the posterior part of the cingulum. At almost all levels, degenerated fibers, as indicated by Marchi granules, passed bilaterally into the corpus callosum, from the corona radiata. A few fine fibers entered the nucleus ventralis posterior pars lateralis bilaterally, but their termination is uncertain. All of these various fascicles spread in the ventral, ventrolateral, lateral, and the dorsolateral tegmentum around the red nucleus or in the red nucleus itself. Some crossing of fibers in the tegmentum was noted.

DISCUSSION

Patterns of body movement elicited by the stimulation of cortical areas other than the precentral motor cortex have been described in primates (Peele, '44; Sugar, Chusid and French, '48; Fleming and Crosby, '55; Travis, '55; Crosby, '56; Crosby, Humphrey and Showers, '59; Schneider and Crosby, '59; and others). The regions that exhibited these movements are both numerous and extensive. They have been named "supplementary motor areas" (Penfield and Welch, '51) or "second" motor areas (Woolsey, '47). The stimulation of

these regions does not produce discrete, highly specialized movements. These second motor areas also have a somewhat greater threshold for excitation than does the motor cortex.

Foerster ('31) reported a pattern of gross body movements from the stimulation of area 6. This pattern was still demonstrable after area 4 had been ablated, which suggested that the movements were a result of independent functioning of area 6. Similar findings have also been reported by Horsley and Schaefer (1888); Vogt and Vogt ('26); Woolsey and Settlage ('50), Erickson and Woolsey ('51), Penfield and Welch ('51), and Travis ('55). The two latter groups of observers amplified this pattern and carried it on to the medial surface of the cerebral hemisphere rostral to the precentral cortex.

Ipsilateral facial movements of both the upper and the lower face, were elicited in monkeys by the stimulation of the precentral gyrus (motor cortex) above the subcentral dimple (Lauer, '52). Similar movements have been found by Garol ('42b) in the cat. Ipsilateral responses of the extremities from stimulation of the motor cortex itself were reported by Bucy and Fulton ('33).

A primary motor eye center, located in area 8 above the principal fissure, has long been known (Vogt and Vogt, '26; Foerster, '31; Penfield and Rasmussen, '50). The pattern of eye movements on it were described by Crosby, Yoss and Henderson ('52) and others. From a portion of the insula in the monkey, Frontera ('55) has also reported the presence of a second motor area. Later, ('56), he regarded this region as concerned largely with visceral functions.

The preoccipital and the occipital regions have shown conjugate horizontal eye deviations upon stimulation. A detailed pattern of eye movements from these regions of the macaque has been described by Crosby and Henderson ('48), Henderson and Crosby ('52), and was reviewed by Crosby ('56).

Corticofugal pathways discharging from some of the supplementary motor areas have been described. Some of these fibers reach lower centers by way of the pyramidal tract. However, a significant num-

ber of extrapyramidal avenues of descent have been found in anatomical and physiological studies (Mettler, '35a, '35b; Levin, '36; Ward, '48; Crosby and Henderson, '48; Meyer, '49; Wall and Davis, '51; Lemmen, '51; Poirier, '51; Jasper, Ajmone-Marsan, and Stoll, '51; and many other observers).

Dusser de Barenne, Garol and McCulloch ('40) reported a discharge pathway from area 5 and the premotor cortex into the putamen and the globus pallidus. From the globus pallidus, fibers course into, and through the lenticular fasciculus and the ansa lenticularis (Woodburne, Crosby, and McCotter, '46; Laursen, '55). Some fibers terminate in the zona incerta and in the nucleus of the field of Forel. However, others continue into the red nucleus, the interstitial nucleus of the median longitudinal fasciculus, the nucleus of Darkschewitsch, and the tegmentum surrounding the red nucleus dorsally, laterally and ventrally. Descending systems from the red nucleus and the midbrain tegmentum into the spinal cord have been well documented.

From the anterior portion of the temporal lobe of *Macaca mulatta*, Poirier ('51) followed fiber bundles into the pulvinar. Crosby ('56) traced degenerated fibers in Marchi preparations from the temporal pole into the putamen and globus pallidus. Lemmen, in 1951, reported projection pathways from areas 19 and 22 into the basal ganglia, the substantia nigra, the red nucleus, and the tegmentum of the midbrain.

The supplementary motor areas appear to function as a region of discharge for association areas which have received impulses from various cortical centers dominated by auditory, visual, gustatory, and olfactory stimuli. Visceral sensory responses and the gross movements of the face and the extremities that are associated with the discrete, specialized motor acts and by which the individual's personality is expressed (Crosby, Humphrey and Showers, '59), may serve as important functions of these areas. The gross movements of the contralateral face and extremities probably are made possible by incomplete substitution of the functioning of additional motor areas for that of primary motor areas, after destruction of the

precentral motor cortex or the pyramidal tract.

Lesions in the frontal, temporal, insular, parietal, and preoccipital cortices were made as a part of this experimental study. From these regions, many avenues of discharge to lower centers were demonstrated in the Marchi preparations of the monkey brains. Cortical association fibers spread from the lesions into the ipsilateral corona radiata and into the white matter of the same hemisphere. Commissural fibers course by way of the corpus callosum into the corresponding regions of the opposite hemisphere.

Corticofugal fibers, as indicated by medium-sized and fine degeneration granules, were traced from the lesions. A few medium and fine fiber bundles from the subcallosal bundle, from the anterior limb of the internal capsule, and from the corona radiata passed into the head of the caudate nucleus in frontal lobe lesions. Here some fibers terminated, but others entered the putamen and or the globus pallidus where they were joined by corticostriate and corticopallidal fibers from the internal capsule. Many of these bundles discharged by way of the globus pallidus or directly into the lenticular fasciculus to end in the zona incerta and in the nucleus of the field of Forel. Other fibers continued to the red nucleus, the interstitial nucleus of the median longitudinal fasciculus, and the nucleus of Darkschewitsch. Some fascicles turned ventrally into the ansa lenticularis through which they entered the tegmentum ventral and caudal to the red nucleus. Corticorubral and corticotegmental fibers, carried in the internal capsule, joined this system and were projected directly into the red nucleus and the tegmentum of the midbrain. In addition, corticorubral and corticotegmental fibers from the corona radiata and the internal capsule entered the nucleus lateralis and nucleus ventralis posterior pars lateralis of the dorsal thalamus. These bundles passed into, and through, the zona incerta and the nucleus of the field of Forel to reach the red nucleus and the tegmentum surrounding this nucleus.

Following frontal, temporal, anterior parietal, and insular lesions, degenerated corticotegmental fibers were traced to the

external capsule. Some of these bundles coursed caudoventrally within this capsule until the external and the extreme capsules became confluent at the posterior part of the putamen. Here the fascicles turned medially, postlenticularly or sublenticularly, over the capsule of the lateral geniculate nucleus and through the posterior limb of the internal capsule, to reach the red nucleus and the tegmentum around it. Fiber contribution from the extreme capsule appeared to add to this projection system but formed a minor component.

Corticotegmental fibers that followed a slightly different course were also noted within the external capsule. From the frontal cortex, degenerated fascicles, indicated by medium and fine granules, entered the external capsule from the corona radiata. At the level of the decussation of the anterior commissure, these fibers turned medialward into the putamen, traveled behind the anterior commissure, and reached the ansa lenticularis to terminate in the tegmentum around and caudal to the red nucleus. In another instance, fiber bundles left the external capsule and turned ventrally toward the base of the hemisphere where some fibers ended in the diagonal band of Broca. The majority of these fibers continued their course dorsally to the ansa lenticularis, the zona incerta, the nucleus of the field of Forel, and the tegmentum around the red nucleus. A few fibers from the extreme capsule passed through the dorsal claustrum to join this system.

Destruction of the posterior parietal and the preoccipital cortices produced degenerated fascicles which were followed into the postlenticular division of the posterior limb of the internal capsule. These corticotectal and corticotegmental bundles coursed through the pulvinar and the posterior part of the nucleus lateralis and the caudal portion of nucleus ventralis posterior pars lateralis of the dorsal thalamus. A few degenerated fibers entered the internal capsule and the globus pallidus where some of these fibers ended. The remainder continued into the ansa lenticularis and the lenticular fasciculus. A very few granules were noted in the caudal part of the external and the extreme capsules. Thus, it appears that the posterior areas

of the brain discharge into the tegmentum postlenticularly, whereas the more rostral regions project primarily into the tegmentum by means of the internal capsule, the basal ganglia, and the external and the extreme capsules.

Following destruction of area 4, coarse and medium Marchi granules were present in the genu and posterior limb of the internal capsule. The degenerated fibers were followed into the pes pedunculi and pyramid ipsilaterally. A few commissural fibers traveled a similar course on the contralateral side. Fiber contributions into the pyramidal tract from the premotor cortex were also noted. A very few fibers from the motor cortex appeared to turn into the globus pallidus and into the external capsule on the side of the lesion, but the great majority of fibers were found in the internal capsule.

Corticopontine fibers from the frontal, parietal, and the temporal cortices were seen. A few corticonigral fibers were traced from the frontal and the temporal lobes into the substantia nigra.

The extreme capsule contained fibers that originated in frontal, parietal, temporal, and insular cortices. These fibers were predominantly cortical association fibers. From the superior, the middle, and the inferior frontal gyri, fibers passed into the uncinata fasciculus to reach the superior and the middle temporal gyri. Other fibers were traced to the inferior temporal and the hippocampal gyri. The frontal lobe was also connected with the insula by fiber bundles that turned out from the extreme capsule. These fibers could not be followed for any considerable distance within the insular cortex due to their extremely delicate myelination.

Degenerated fibers from lesions of the parietal cortex were traced into the extreme capsule. Cortical association fibers interconnected the parietal and the temporal lobes. A few bundles entered the insular cortex. These also were extremely fine fascicles that were soon lost.

Following lesions of the superior and the middle temporal gyri, degenerated fibers were demonstrable in the extreme capsule. These traveled in the uncinata fasciculus to the frontal operculum. Also temporoparietal fibers were seen within the ex-

treme capsule. A few delicate fascicles turned laterally into the insular cortex.

After destruction of portions of the island, medium and fine Marchi granules were followed into the extreme capsule. Many of these bundles turned dorsally to reach the inferior frontal gyrus. Cortical association fibers interconnected the insula with the temporal lobe.

Although the great majority of fibers in the extreme capsule are cortical association bundles, a very few corticotegmental fibers were found. These fibers worked their way caudoventrally within their capsular boundary until the external and the extreme capsules became confluent at the caudal end of the putamen. At this point, the fascicles joined corticotegmental fibers in the external capsule and turned postlenticularly or sublenticularly over the capsule of the lateral geniculate nucleus and through the posterior limb of the internal capsule to project into the tegmentum around the red nucleus. A few fibers were exchanged between the external and the extreme capsule passing through the dorsal claustrum. Whether any of these fibers terminated in the claustrum could not be determined with certainty.

The frontal and the parietal lobes contributed fibers to the extreme capsule from the corona radiata. From the temporal lobe and the island, fascicles also reached the external capsule after passing through the extreme capsule and the claustrum.

The external capsule contained a few cortical association bundles from the extreme capsule. However, cortical projection fibers formed its major components. These arose from the frontal, parietal, insular, and temporal lobes. Finely medullated fibers coursed medially from the external capsule into the lateral border of the putamen. Such fibers were not numerous and could be traced only for short distances due to their extremely delicate myelin sheaths. An avenue of cortical projection to lower centers is found then in the external capsule, which is conveniently situated as a pathway for the discharge of supplementary motor areas. Some degenerated fibers, as indicated by medium and fine degeneration granules, turn medially, leave the external capsule, and enter the ventral part of the putamen at anterior

commissure levels. These bundles continue their course into the globus pallidus toward the ansa lenticularis; some terminate in the zona incerta or in the nucleus of the field of Forel, others extend beyond into the tegmentum around the red nucleus as a part of the corticotegmental discharge system.

Fascicles in the external capsule extend toward the base of the hemisphere. Here some fibers end in the diagonal band of Broca. Most of these fibers, however, turn dorsally into the ansa lenticularis to reach the tegmentum around the red nucleus.

Still, a third corticotegmental pathway enters the external capsule. These corticofugal fibers gradually work their way caudoventrally within their capsular boundary until the external and the extreme capsules become confluent at the caudal end of the putamen. Here these fibers are joined by the few additional bundles that remain in the extreme capsule. Together, these fascicles travel medially, postlenticularly and then sublenticularly, over the capsule of the lateral geniculate nucleus and through the posterior limb of the internal capsule, to end in the tegmentum around the red nucleus.

From frontal lesions, some fiber bundles course caudally into the superior longitudinal fasciculus and accumulate at parietal levels. Many of these then swing into the region of junction of the external and the extreme capsules and pass ventromedially across the dorsal tip of the putamen to reach the posterior limb of the internal capsule. These fibers presumably add in part to the corticotegmental discharge system.

The claustrum, in the beginning of this study, was regarded as a possible region of synapse in the relay for the discharge of extrapyramidal systems from the cortical second motor areas to the tegmentum of the midbrain and the reticular gray. Apparently, this relation is not demonstrable.

Fibers from frontal, temporal, and insular areas sweep into the claustral region. The external and the extreme capsules exchange fibers through the dorsal claustrum. In this experimental material, there is some evidence that temporal area 22, the premotor, and the more rostral portions of the frontal cortex contribute to the claus-

trum. However, the majority of these fascicles are fibers of passage. Whether any fibers terminate in the claustrum is still questionable.

Collaterals from the extreme and the external capsules probably end near claustral cells. However, silver preparations showed a tangled network of indistinct fibers, giving no support to this idea. The Marchi material in this study did not contribute any additional information in this regard due to the extremely fine myelin sheaths that the claustral fibers possess. The claustrum may offer some fiber contributions to the external and the extreme capsules, to insular cortex, and to the putamen. Experimental proof for this concept is still lacking.

Mettler, Ades, Lipman, and Culler ('39) inhibited a cortically evoked movement by simultaneous stimulation of cortex and claustrum. Kaada ('51) obtained similar results from excitation of the claustrum of cats and monkeys. The present material is not able to add much anatomical evidence to substantiate these results.

If corresponding pathways exist in human brains, the corticotegmental fibers that discharge through the external and the extreme capsules assume clinical importance with the destruction of the genu and the posterior limb of the internal capsule due to hemorrhage or degenerative processes. Lesions of these types involve both the pyramidal tract and the extrapyramidal fibers projecting through the internal capsule and through the basal ganglia by way of the lenticular fasciculus. Voluntary, highly specialized movements of the contralateral face and the extremities are lost as a result. Remaining functions become dependent upon the degree of substitution that is possible by means of the unimpaired projection systems from the supplementary motor areas relaying through the external and the extreme capsules into the tegmentum of the midbrain. Although the corticorubral and the corticotegmental fibers from individual second motor areas are not numerous, altogether, these fibers constitute a considerable discharge system.

SUMMARY

From the areas studied, fibers that terminate in the claustrum are not numerous.

Probably short collaterals are exchanged with the insular cortex and the basal ganglia. Area 22, premotor cortex, and frontal areas rostral to the precentral gyrus contribute fibers to the claustrum. Most of these are fibers of passage. Silver preparations showed no definite fibers beginning or ending within the claustrum.

The external capsule is composed primarily of corticotegmental fibers. A few cortical association fibers are present.

The extreme capsule is primarily a cortical association bundle interconnecting frontal, insular, and temporal cortices. Parietal and temporal lobes also exchange fibers through it.

The external capsule assumes importance due to the fascicles it receives from area 4 and from the supplementary motor areas as discharge pathways into the tegmentum of the midbrain. It becomes clinically significant when lesions of the genu and the posterior limb of the internal capsule and destruction of the basal ganglia occur. In the external capsule a considerable number of fibers are spared which may make gross motor responses possible through their discharge to motor centers by way of the tegmentum.

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PLATE 1

EXPLANATION OF FIGURES

- 1 Brain 1. Ablation of areas 4 and 6 on left side. Right lesion involves areas 6, 8 and 9.
- 2 Brain 2. Lesion in areas 6 and 9 of the left hemisphere.
- 3 Brain 3 showing lesions of the left hemisphere anterior and posterior to the arcuate fissure. A second lesion in the sensory cortex is also noted.
- 4 Brain 4 showing a lesion of left area 11.
- 5 Brain 5 demonstrating an area 4 lesion of the right hemisphere.
- 6 Brain 5 showing left sided lesions of the frontal and temporal opercula. An insular lesion has also been made.

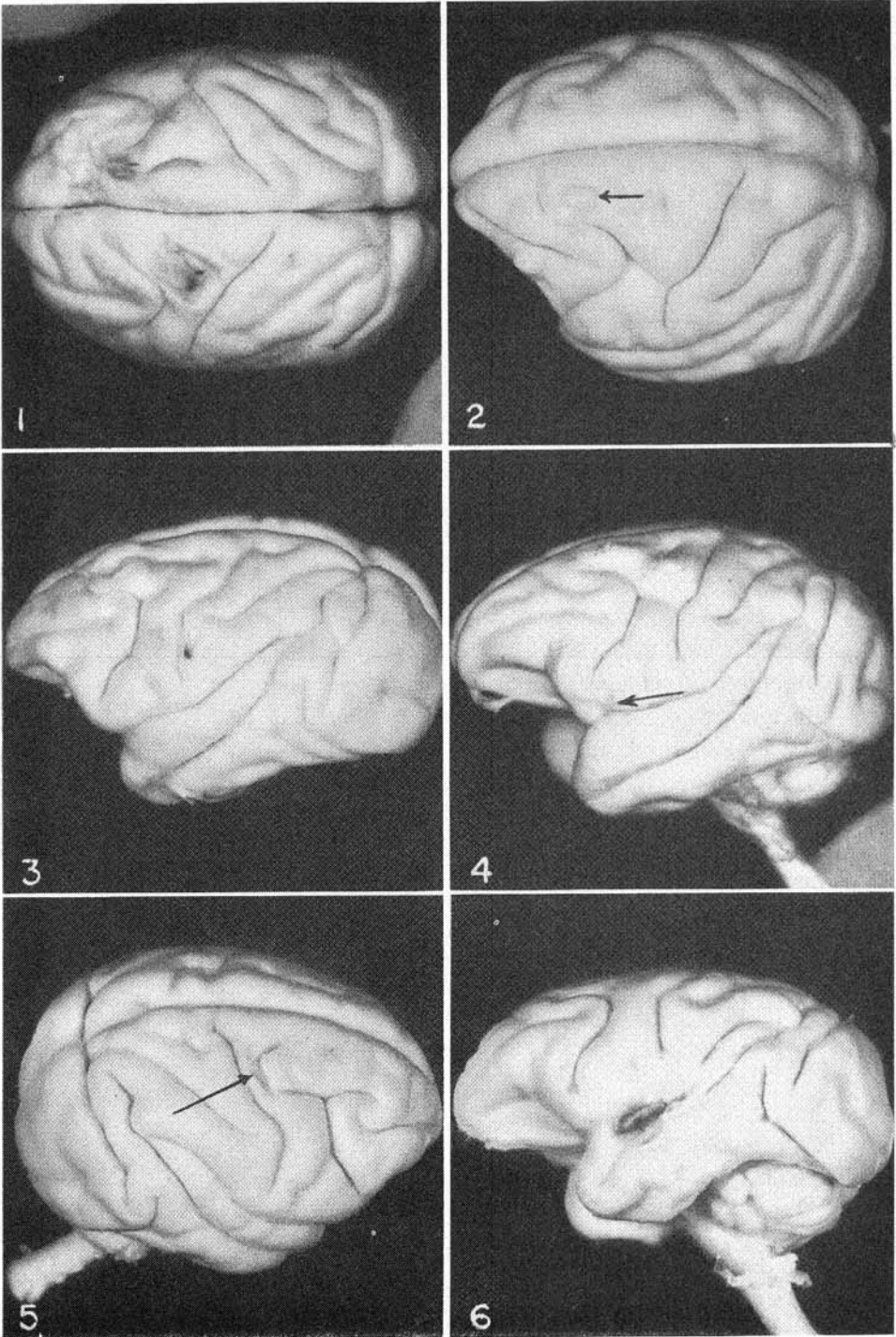


PLATE 2

EXPLANATION OF FIGURES

- 7 Brain 6 showing lesion of area 8.
- 8 Brain 6 showing a left superior temporal lesion.
- 9 Brain 7 demonstrating a left area 22 lesion.
- 10 Brain 7 with lesion of right area 22.
- 11 Brain 8 showing a lesion of area 7.
- 12 Brain 9 showing lesions in area 5 and preoccipital cortex of the left hemisphere.

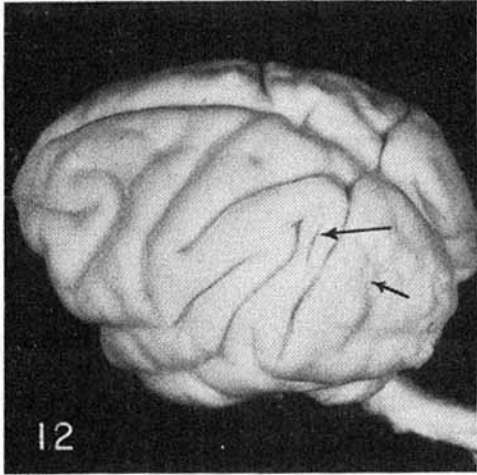
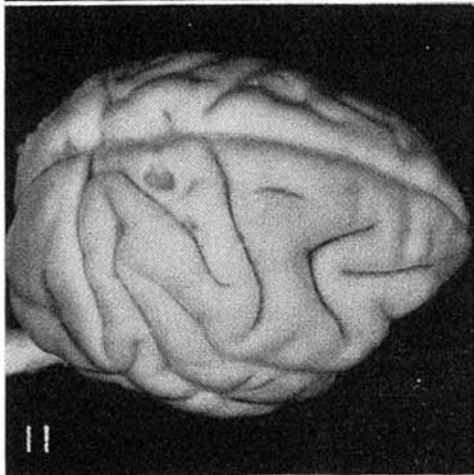
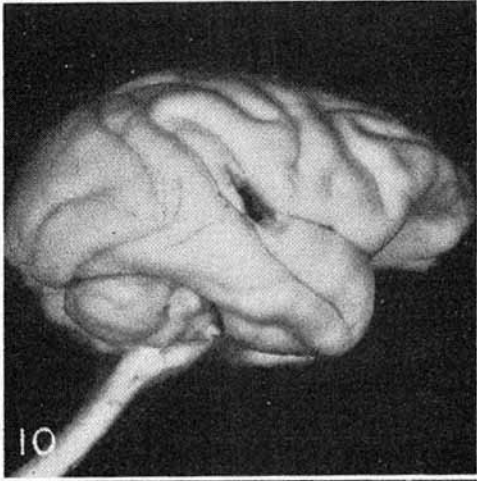
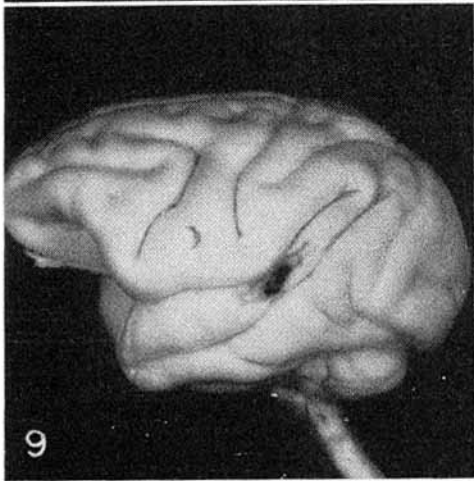
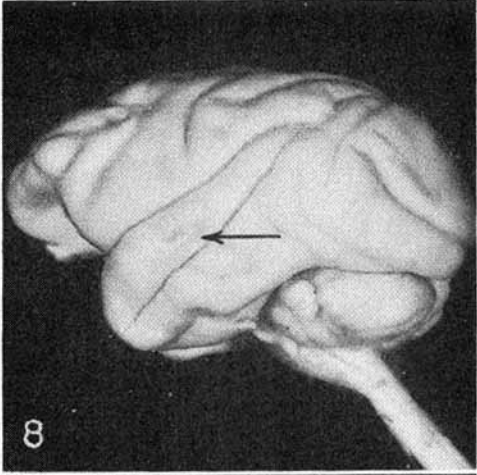
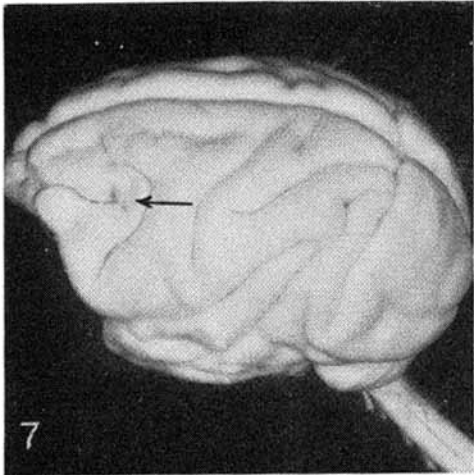


PLATE 3

EXPLANATION OF FIGURES

- 13 Photomicrograph showing Marchi degenerating fibers coursing from the caudate nucleus into the putamen by way of the gray bridges. C, caudate nucleus; I, internal capsule; P, putamen. Brain 1. Marchi stain. $\times 17.5$.
- 14 Photomicrograph showing degeneration granules in the red nucleus (R), and the tegmentum surrounding the red nucleus. T, tegmentum; O, oculomotor nerve; R, red nucleus. Brain 1. Marchi stain. $\times 35$.
- 15 Photomicrograph showing degeneration in the lenticular fasciculus (L) and in the internal capsule (I). Brain 1. Marchi stain. $\times 35$.
- 16 Photomicrograph showing degenerated fascicles from the combined external and extreme capsules (C) passing caudal to the putamen (P) to the posterior limb of the internal capsule (I). Brain 1. Marchi stain. $\times 50$.
- 17 Photomicrograph demonstrating Marchi granules in fascicles coursing over the capsule of the lateral geniculate nucleus (L.G.) into the tegmentum of the midbrain. D.T., dorsal thalamus; I, internal capsule. Brain 1. Marchi stain. $\times 17.5$.
- 18 Comparison of the pyramids (P) bilaterally. Brain 1. Marchi stain. $\times 17.5$.

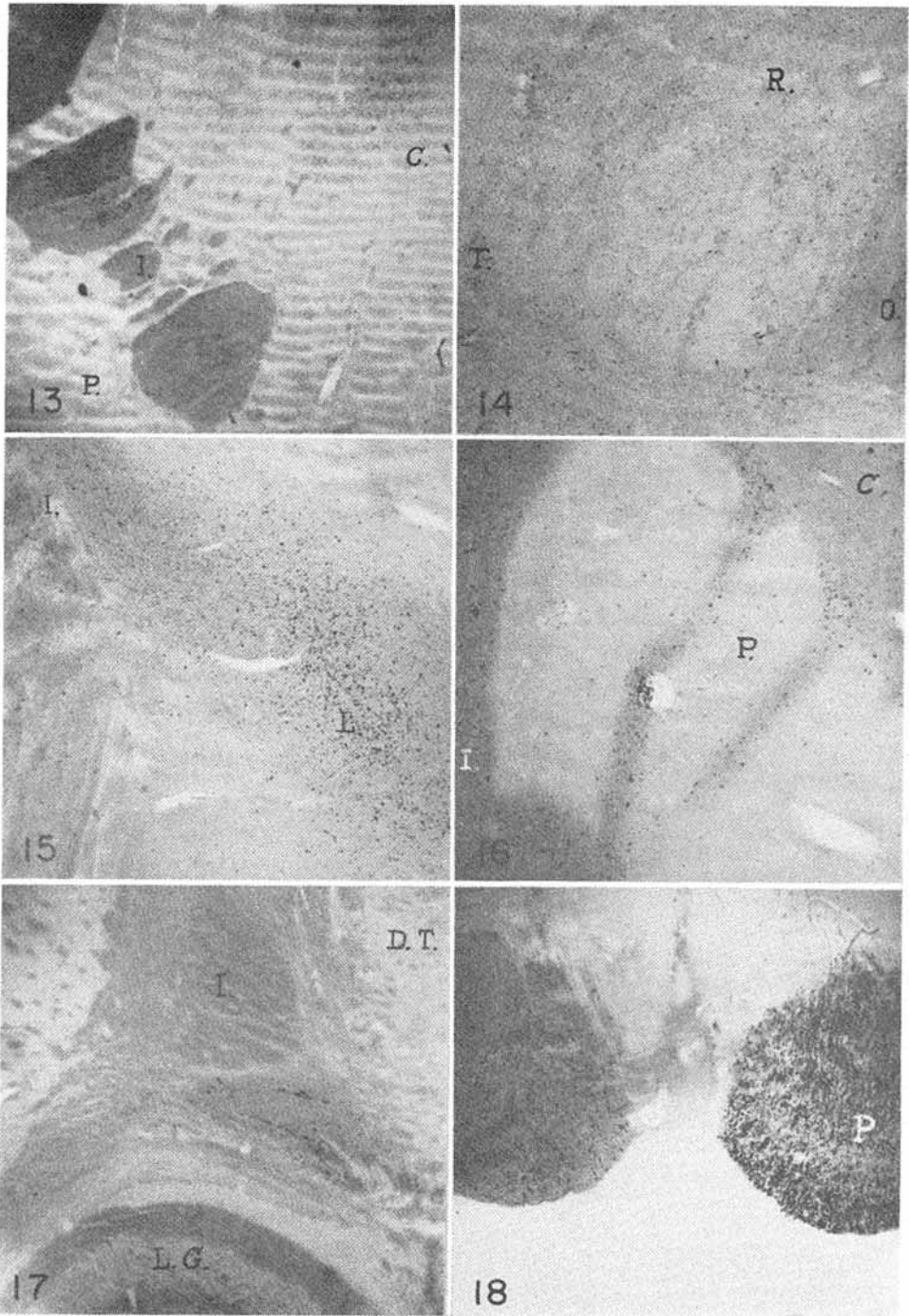


PLATE 4

EXPLANATION OF FIGURES

- 19 Photomicrograph showing Marchi granules in fascicles (arrows) leaving the external capsule (E.c.). C, claustrum; Ex. c., extreme capsule; I, insula; P, putamen. Brain 2. Marchi stain. $\times 17.5$.
- 20 Photomicrograph showing degeneration granules in the lenticular fasciculus (L). I, internal capsule. Brain 3. Marchi stain. $\times 35$.
- 21 Photomicrograph showing Marchi granules in fascicles (arrow) coursing at the base of the hemisphere (B.H.). A, anterior commissure. Brain 2. Marchi stain. $\times 17.5$.
- 22 Photomicrograph showing Marchi granules in fibers passing across the ventral portion of the putamen (P). A, anterior commissure. Brain 3. Marchi stain. $\times 35$.
- 23 Photomicrograph showing Marchi granules in fascicles (arrows) turning into the ansa lenticularis. G, globus pallidus; O, optic tract. Brain 2. Marchi stain. $\times 17.5$.
- 24 Photomicrograph showing Marchi granules in the external capsule (E). Some of these course into the putamen (P), others continue within the external capsule. C, claustrum. Brain 3. Marchi stain. $\times 50$.

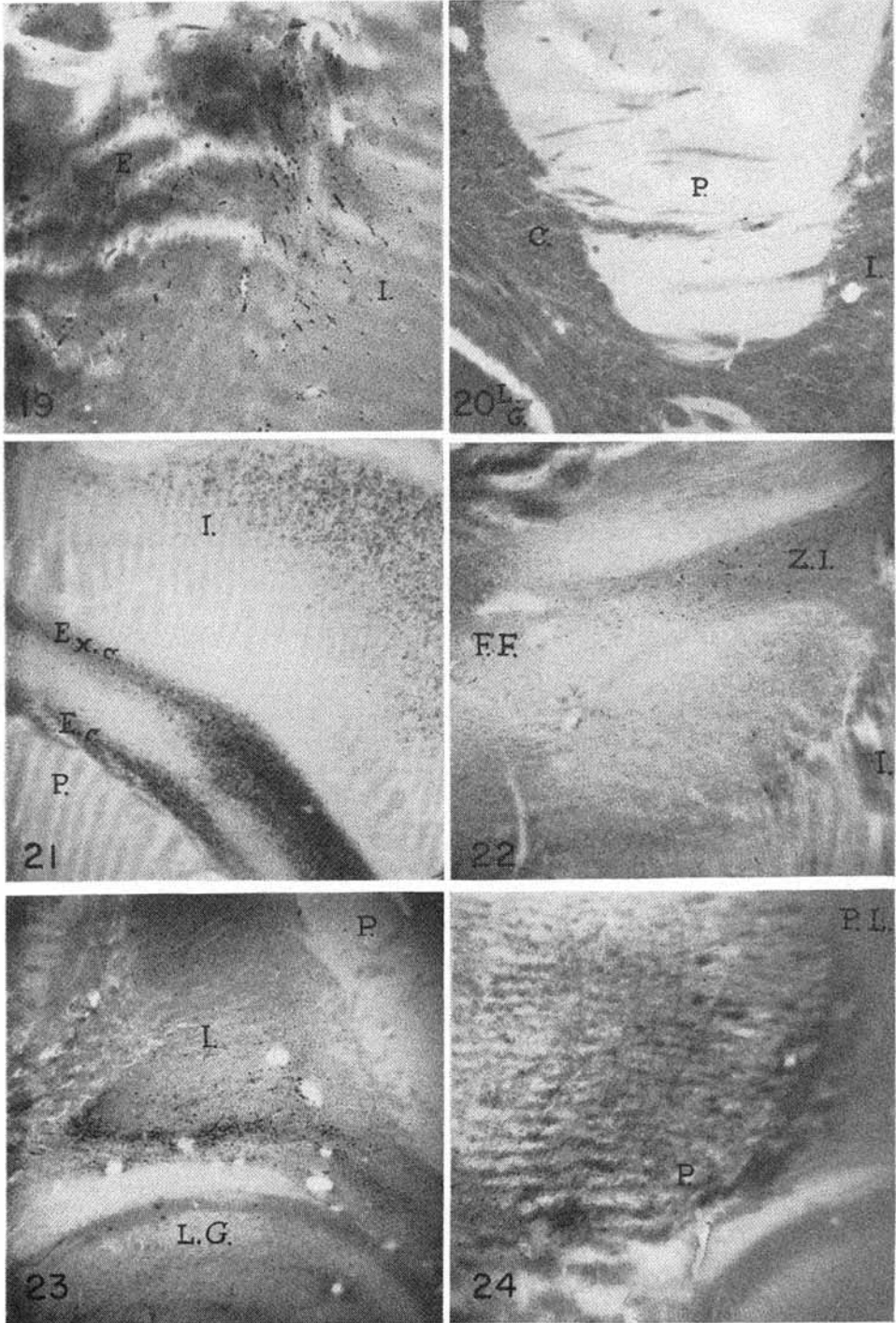


PLATE 5

EXPLANATION OF FIGURES

- 25 Photomicrograph showing Marchi granules in fibers entering the extreme capsule (E) from the insula (I). Brain 4. Marchi stain. $\times 50$.
- 26 Photomicrograph showing Marchi granules in sublenticular fascicles from the common external and extreme capsules (C) coursing toward the posterior limb of the internal capsule (I). P, putamen; L. G., lateral geniculate nucleus. Brain 4. Marchi stain. $\times 35$.
- 27 Photomicrograph showing an insular lesion with degeneration from the insula (I) and massive destruction of the extreme (Ex.C.) and the external (E.c.) capsules. P, putamen. Brain 5. Marchi stain. $\times 35$.
- 28 Photomicrograph showing degeneration granules in the lenticular fasciculus, zona incerta (Z.I.) and the nucleus of the field of Forel (F.F.) Brain 5. Marchi stain. $\times 17.5$.
- 29 Photomicrograph showing degeneration granules over the capsule of the lateral geniculate nucleus (L.G.) to enter the tegmentum of the midbrain. I, internal capsule; P, putamen. Brain 5. Marchi stain. $\times 17.5$.
- 30 Photomicrograph showing degenerated fascicles coursing across the pulvinar (P.). P.L., posterior limb of the internal capsule. Brain 8. Marchi stain. $\times 17.5$.

